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The Latitudinal Distribution of Morphological Diversity among Holocene Angiosperm Pollen Grains from eastern North America and the Neotropics

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Running title: Latitudinal distribution of angiosperm morphological diversity

Abstract

Current knowledge about the biogeographic patterns of biodiversity is based mostly on taxonomic diversity, which is typically measured as the number of species or higher taxa. In this paper I analyse 26 previously published Holocene lake core pollen records in order to assess how the morphological diversity of angiosperm pollen grains varies with latitude on a transect that includes eastern North America and the Neotropics. This represents a step towards understanding the evolution of plant morphology in a biogeographical context. I employ a system of eight discrete characters to describe first-order features of angiosperm pollen morphology and use algorithms written in the Python programming language to assess their morphological diversity. There is no statistically significant relationship between taxonomic diversity and morphological diversity in the samples of Holocene angiosperm pollen investigated here. The number of pollen morphotypes in the sediment samples investigated here increases from high latitudes to the tropics, but the highest morphological diversity occurs at high latitudes, and the lowest morphological diversity occurs at mid-latitudes around 40–50°N. At the biome level, there are peaks in morphological diversity at low and high latitudes with a trough in mid latitudes. There is evidence of high levels of pollen morphotype endemism in the tropical biome, and further work on how the volume of morphological space varies with latitude is needed in order to understand whether taxa in species-rich tropical ecosystems are more densely packed into morphological space.

Introduction

Current knowledge about the biogeographic patterns of biodiversity is based mostly on taxonomic diversity, which is typically measured as the number of species or higher taxa (Roy et al. 2001). One first-order pattern that has been revealed by studying the biogeographic distribution of taxonomic diversity is the latitudinal diversity gradient (LDG), which describes the observation that the tropics generally contain considerably more species than higher latitudes (Wiens and Donoghue 2004). This pattern is almost ubiquitous among higher taxa, and among plants it has been shown that increasing taxonomic diversity with decreasing latitude is ancient and stretches as far back in time as the Paleocene/Eocene ~56 Million-Years-Ago (Harrington 2004, Jardine et al. 2012).

An alternative measure of biodiversity is morphological diversity, which is an outstandingly intuitive measure of biological variety, and can provide data on biodiversity in situations where an estimate of phylogeny is either absent or unreliable (Roy and Foote 1997). However, "for most groups of living organisms very little data exist on how spatial patterns of species richness relate to similar trends in morphological diversity" (Roy et al. 2001, p. 2503). This is certainly true for plants, and in this short exploratory paper I use fossil pollen grains of flowering plants to examine how morphological diversity varies with latitude on a transect from eastern North America to the Neotropics. This represents a step towards understanding how plant form has evolved in a biogeographical context, and provides a starting point for analyses of how competition, speciation and extinction, as well as phylogenetic constraints, control the spatial distribution of morphology in plants.

The specific aims of this study are as follows: (1) to examine how the taxonomic diversity and morphological diversity of pollen grains compare to one another; (2) to describe how morphological diversity among Holocene pollen grains varies with latitude on a transect from eastern North America to the Neotropics; and (3) to determine whether pollen grains provide any evidence for plant endemism in the Neotropics.

Materials and Methods

Sites and samples

The raw materials for this study are 26 previously published Holocene lake core pollen records from eastern North America and the Neotropics. These pollen records were extracted from the Neotoma online database (<https://www.neotomadb.org/>) and they span a latitudinal transect from 0° to 78°N (see Table 1). I extracted counts of fossil pollen grains from two sediment samples in the 2,500–3,500 year interval of each sediment core. This number of samples and time interval was chosen to follow the sampling strategy of Jardine et al. (2012), which avoids early Holocene climate change and substantial human landscape alteration in the later Holocene (Mayle et al. 2000; Williams et al. 2000). If more than two sediment samples were available in this time interval, I selected the sample closest to 2,500 years and the sample closest to 3,500 years.

The raw count data in each of the two sediment samples was pooled, and I removed spores, gymnosperm pollen grains, unidentified angiosperm pollen, and taxa in open nomenclature. The trimmed datasets were combined into one matrix, and the lists of taxa in each site were standardized to one another by grouping species into genera following Harrington (2004). The resulting data

matrix consists of angiosperm pollen grains identified mostly at the family and genus level (see Supplementary Information).

Describing angiosperm pollen morphology

Each pollen grain taxon in the dataset was scored for the following eight discrete morphological characters based on those developed by Mander (2016):

apertures (21 character states), aperture variation (two states), aperture operculum (two states), exine stratification (two states), equatorial diameter (five states), polar outline (four states), dispersal unit (six states), and surface ornamentation (20 states). This scoring was undertaken using descriptions in the online pollen morphology database PalDat (<https://www.paldat.org/>) and the published literature. Scoring pollen grains involved reading descriptions and inspecting images of pollen grains. For the tropical sites, the monographs of Roubik and Moreno (1991) and Colinvaux et al. (1999) were consulted in addition to the PalDat database. Pollen grains were only scored for features observable using a light microscope rather than an electron microscope.

Pollen grains were only scored for primary surface ornamentation (see Mander 2016 for a discussion of primary and secondary surface ornamentation in angiosperm pollen). In the Cyperaceae, the pseudotetrad condition in this family was scored as a monad, and *Nymphaea* was scored as monoporate with an operculum. For the Rosaceae, Polygonaceae and Sapindaceae, a single scoring for the family was produced based on comprehensive general family-level characteristics given in Hebda and Chinnappa (1994) and Hong et al. (2005), respectively. In the absence of such general characteristics, taxa that were classified only to the family level were scored as an exemplar genus, usually the

type genus: Acanthaceae (*Acanthus*), Anacardiaceae (*Anacardium*), Apiaceae (*Apium*), Apocynaceae (*Apocynum*), Arecaceae (*Areca*), Boraginaceae (*Borago*), Combretaceae (*Combretum*), Euphorbiaceae (*Euphorbia*), Lamiaceae (*Lamium*), Loranthaceae (*Loranthus*), Rubiaceae (*Rubia*), Rutaceae (*Ruta*), Sapindaceae (*Sapindus*), Sapotaceae (*Manilkara*), Solanaceae (*Solanum*). Caesalpinioideae scored from Banks and Lewis (2009), Salicaceae was scored as *Hasseltia* and Spermacoce was scored as *Spermacoce tenuoir* (see Roubik and Moreno 1991; Mander 2016).

Measuring morphological diversity

Following scoring for each of the eight discrete characters, the morphology of each pollen grain in the dataset was encoded in a string of length 8.

Morphological distance between species was measured by computing the Hamming distance between their character state strings. The Hamming distance between two strings of equal length can be defined as the number of positions at which the corresponding characters are different, and it is frequently used to detect errors in code (Hamming 1950) and to measure the distance between genetic sequences (Pilcher et al. 2008). As an example, consider the following two taxa from the data set used in the present paper and the strings (contained in brackets) that encode their morphology:

Poaceae=(2,2,1,2,3,1,1,2)

Quercus=(10,1,2,2,3,1,1,2)

In the language of descriptive palynology (Punt et al. 2007), these strings contain the following morphological information. The grass (Poaceae) has a pollen grain that is monoporate (2), with an aperture that has a variation in the

form of an annulus (2) and also has an operculum (1), is tectate (2), measures 30–45µm in equatorial diameter (3), is circular in polar outline (1), is dispersed as a monad (1) and has scabrate surface ornamentation (2) (Fig. 1A, B). The oak (*Quercus*) has a pollen grain that is tricolpate (10), with no aperture variation (1) and no aperture operculum (2), is tectate (2), measures 30–45µm in equatorial diameter (3), is circular in polar outline (1), is dispersed as a monad (1) and has scabrate surface ornamentation (2) (Fig. 1C, D).

The two strings that encode the morphology of these species, (2,2,1,2,3,1,1,2) and (10,1,2,2,3,1,1,2), differ at 3 positions and so the Hamming distance between them is 3. In this paper, Hamming distances are reported as proportions, which in this example is 0.375 because the strings are of length 8. When converted to a proportion in this way, the Hamming distance is equivalent to 1–SMC, where SMC is the Simple Matching Coefficient that has been used in several previous studies of morphological diversity (e.g. Foote 1994, Lupia 1999). In this paper, the term morphological diversity is synonymous with the term morphological disparity that has been used by other authors (e.g. Foote 1994, Lupia 1999). The morphological diversity of each sample and each biome is reported principally as the mean pairwise Hamming distance, but I have included maximum range as a comparator (see Foote 1994, Lupia 1999). These computations were undertaken using the Python programming language and algorithms are available in the Supplementary Information.

Results

Discrete characters and plant diversity

The system of eight discrete characters that I have used to describe angiosperm pollen morphology produces morphotypes that do not include subtle morphological details such as the size and density of sculptural elements on the pollen surface. Instead, morphotypes are separated by first-order morphological differences such as the type of aperture or the class of surface ornamentation. Consequently, the taxonomic diversity of each site as measured by these morphotypes is lower than the taxonomic diversity measured by the raw pollen count data. For example, the highest latitude site (78°N) contains 15 taxa but 14 pollen morphotypes, and a low latitude site (5°N) contains 44 taxa but 40 pollen morphotypes. Despite this however, among the suite of 26 sites there is a positive relationship between the number of taxa recorded in the raw count data and the number of pollen morphotypes produced by the system of discrete characters I have employed (Fig. 2).

Taxonomic versus morphological diversity

In the 26 sites investigated here, the number of pollen morphotypes varies from nine to 40 (Table 1). However, there is no clear relationship between a sample's taxonomic diversity, as measured by the number of pollen morphotypes, and its morphological diversity (Fig. 3). Morphological diversity, as measured by mean pairwise Hamming distance, varies from 0.5 at a site that contains 11 morphotypes (Iglutalik Lake at 66°N) to 0.38 at a site that contains 23 morphotypes (Stages Pond at 40°N) (Fig. 3, Table 1). Morphological diversity as measured by the maximum Hamming distance range at a site is also independent of taxonomic diversity. For example, the maximum Hamming distance range of

Stages Pond (23 morphotypes) is 0.625 but the maximum Hamming distance range of Langdale Pond (24 morphotypes) is 0.875 (Table 1).

Taxonomic and morphological diversity at different latitudes

Taxonomic diversity, as measured by the number of pollen morphotypes, is greater in samples from the tropics than in samples from higher latitudes (Fig. 4). However, the same is not true for morphological diversity. For example, the Lake Chenevo site at 5°N has the joint highest taxonomic diversity in the dataset investigated here, but it does not contain the highest levels of morphological diversity (Table 1). Instead, the highest morphological diversity occurs at high latitudes, and the lowest morphological diversity occurs at mid-latitudes around 40–50°N (Fig. 5). When the sites are pooled into biomes (see Table 1 for the biome boundaries used in this paper), morphological diversity is lowest in the temperate biome, and increases towards the tropical biome and the tundra biome (Fig. 6, Table 2).

Discussion

Among the sites investigated here, the difference between the highest morphological diversity and the lowest morphological diversity is 0.115 (Iglutalik Lake versus Stages Pond) (Table 1). To place this difference into context, if two pollen grains described by strings of length 8 differ at one position then the Hamming distance between them is 0.125. The two sites that differ by 0.115 in terms of mean pairwise Hamming distance therefore differ by almost an entire character in morphological terms. Similarly, the sites that differ by 0.25 in terms of maximum Hamming distance range (Stages Pond [0.625] and Langdale

Pond and Lake Chenevo [both 0.875] (Table 1)) differ by two whole characters in morphological terms. Given the relatively coarse resolution of the discrete characters I have employed here, such differences correspond to substantial first order morphological differences. This is important because it demonstrates that the Hamming distance, whether reported as mean pairwise distance or as maximum range, is capable of capturing variation between sites and between biomes that is substantial in morphological terms.

A clear source of potential error in the description of how morphological diversity varies on the latitudinal transect investigated here (Fig. 5, Fig. 6) is the variable taxonomic resolution of the raw pollen count data (see Mander and Punyasena 2014 for a review). For example, the raw count data report Fabaceae and Rubiaceae at the family level at several sites with no indication of how many different pollen types referable to these families were encountered (see Supplementary Information). In the absence of any other information I have reduced the morphology of these families to a single exemplar genus, and this represents a gross oversimplification given that pollen morphology in the Fabaceae and Rubiaceae is enormously diverse, particularly in the tropics (e.g. Mander 2016). It has been shown that spatial patterns in plant diversity such as the LDG are observable at high taxonomic ranks such as family (Qian and Ricklefs 2007), but if work on the biogeography of pollen morphology were to be undertaken using primary data gathered from palynological slides, with individual pollen grains scored for discrete characters when viewed using a microscope, then the variable taxonomic resolution of data derived from the published literature could be overcome.

Pollen grains are dispersed from their parent plant and are transported primarily by wind, water and animal vectors to a variety of depositional centres that range from lakes and fluvial settings to swamps and marine environments (Gastaldo 2001, Traverse 2007). The samples investigated here are all derived from lakes, there are no samples from fluvial deposits such as the Late Quaternary Tunica Hills region of the southern United States (Jackson and Givens 1994) for example, and this represents an attempt to exert a degree of control over one aspect of the sampling strategy in this paper. However, assemblages of fossil pollen grains deposited in lakes contain some specimens produced by plants growing in the immediate vicinity of the lake, such as the plants growing at the lake margin, as well as specimens produced in a source area around the lake, as well as long distance transport of widely dispersed pollen grains that can be transported across continents (Davis 2000). Such a mixture of local, regional and long-distance pollen is not thought to be fatal to the reconstruction of vegetation history using fossil pollen grains. This is because empirical studies that compare mapped patterns of present-day tree pollen percentages to the geographic patterns of relative tree abundance (e.g. Webb 1974; Prentice et al. 1987) and theoretical studies of pollen dispersal (Prentice 1985; Sugita 1993, 1994) both indicate that, as a first approximation, changes in pollen percentages in samples through time can be interpreted in terms of roughly comparable changes in relative abundances of taxa in the source vegetation (Prentice and Webb 1986; see Mander and Punyasena 2018 for a review). However, similar work has not been done on how the morphological landscape, at the level of pollen grains, is reflected in assemblages of fossils. It is possible that transport of pollen grains from different biomes may artificially increase or decrease

morphological diversity, and this may occur frequently at sites that are situated close to biome boundaries.

Another source of potential error in the description of how morphological diversity varies with latitude is the limitation of discrete characters themselves. Notwithstanding the fact that the measures of morphological distance used here can delineate substantial variation in morphological diversity between sites and biomes, it is clearly the case that a system of just eight discrete characters is limited in terms of the amount of morphological variation it can capture. For example, the genus *Brasenia* (Cabombaceae) produces pollen with a highly distinctive horsehoe-shaped colpus (Remizowa et al. 2008), but this genus is simply scored "monocolpate" along with several other taxa in this analysis. Increasing the number of character states would allow such detailed variation in pollen morphology to contribute to the overall patterns of morphological diversity between sites and biomes and across latitude.

These sources of potential error mean that the results of the analyses in this paper (e.g. Fig. 5 and Fig. 6) should be interpreted with caution. However, it is possible that these descriptions of the latitudinal distribution of morphological diversity reflect the true underlying biogeographic pattern. Assuming this to be the case, the presence of comparable levels of morphological diversity across the wide latitudinal and ecological range studied here (Fig. 5), with a possible peak in low and high latitudes and a trough in mid latitudes (Fig. 6), raises questions about its origin. On the assumption that morphology indicates ecological position (e.g. Ricklefs 2012), processes such as competition can determine patterns of morphospace occupation, but at regional scales such as those involved here, speciation and extinction generate morphological diversity, and the distribution

of species in morphological space is also partly constrained by phylogeny (Roy et al. 2001).

Just four pollen morphotypes are found in all five biomes, and these are either generalized forms produced by several taxa, such as the tricolpate reticulate pollen produced by the Brassicaceae, Lamiaceae and *Fraxinus*, or morphotypes produced by plant families found in all five biomes, such as monoporate pollen produced by the Poaceae, tricolporate echinate pollen produced by the Asteraceae, and pantoporate pollen produced by the Cyperaceae. Additionally, while noting that the "spillover" of taxa from tropical regions into higher latitudes influences historical richness gradients (Harrington 2004), there is evidence of high levels of pollen morphotype endemism in the tropical biome (Fig. 7; in this paper endemic morphotypes are those that are restricted to one of the five biomes). I interpret these biogeographic patterns as reflecting the outcome of plant diversification in the tropics that is largely independent of diversification at higher latitudes, and suggest that the decoupling of taxonomic and morphological diversity, both at the site and biome level, indicates that taxa in species-rich tropical ecosystems may be more densely packed into morphological space than taxa in relatively species-poor ecosystems at higher latitudes (cf. Ricklefs 2012 for passerine birds).

Further work should consider how the volume of morphological space occupied by pollen grains changes with latitude in order to explicitly test this hypothesis. Such work could include comparison of taxonomic, morphological as well as phylogenetic diversity, as well as a more uniform sampling of each biome, which is very uneven in this present paper. In particular, there are >20° of latitude separating the samples from the tropical biome and the samples from

the subtropical biome, and this is an additional possible explanation for the high proportion of pollen morphotypes that are endemic to the tropical biome in the analyses reported here.

Concluding Remarks

This paper represents an exploratory analysis of how the morphological diversity of angiosperm pollen grains varies with latitude, and the following conclusions can be drawn:

(1) A system of eight discrete characters has been used to describe first-order features of fossil angiosperm pollen morphology in 26 previously published lake cores from the Holocene of North America and the Neotropics. There is a positive relationship between the number of taxa recorded in the raw count data from these samples and the number of pollen morphotypes produced by the system of discrete characters employed here (Fig. 2). However, it should be kept in mind that the raw pollen count data contains a mixture of taxa identified to generic level and higher. Consequently, Figure 2 does not necessarily indicate that pollen data captures true Holocene plant diversity in the original standing vegetation, only that there is an interpretable relationship between the count data and the morphotyping system I have employed in this paper.

(2) In the 26 sites investigated in this paper there is no statistically significant relationship between a sample's taxonomic diversity, as measured by the number of pollen morphotypes, and its morphological diversity as measured by the mean pairwise Hamming distance (Fig. 3). This is similar to previous work

on marine macrofauna, which has demonstrated a similar decoupling of taxonomic and morphological diversity (Roy et al. 2001).

(3) The number of pollen morphotypes in the sediment samples investigated here increases from high latitudes to the tropics (Fig. 4). In contrast, the highest morphological diversity occurs at high latitudes, and the lowest morphological diversity occurs at mid-latitudes around 40–50°N (Fig. 5). When the sites are pooled into biomes, there are peaks in morphological diversity at low and high latitudes with a trough in mid latitudes (Fig. 6).

(4) There is evidence of high levels of pollen morphotype endemism in the tropical biome (Fig. 7), and further work on how the volume of morphological space varies with latitude is needed in order to address the hypothesis that taxa in species-rich tropical ecosystems may be more densely packed into morphological space than those in species-poor ecosystems at higher latitudes (cf. Ricklefs 2012).

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Figure Captions

Figure 1. Oak pollen imaged with scanning electron microscopy (A) and transmitted light microscopy (brightfield illumination, B). Grass pollen imaged with scanning electron microscopy (C) and transmitted light microscopy (brightfield illumination, D). Arrows in each image highlight differences in the apertures of these two pollen types. The arrow in A and B highlights one of the three colpi—apertures that are shaped as narrow slits—that characterise oak pollen. The arrow in C and D highlights the single pore with annulus and operculum that characterises grass pollen. Scale bars represent 10µm.

Figure 2. Plot illustrating the positive relationship between the number of taxa and the number of pollen morphotypes in the samples studied here. Each data point represents a single site (see Table 1 for details). This relationship is statistically significant (Kendall's Tau = 0.939, $p < 0.001$).

Figure 3. Plot comparing morphological diversity and the number of pollen morphotypes in the samples investigated here. Morphological diversity measured by mean pairwise Hamming distance. There is no statistically significant relationship between these two variables (Kendall's Tau = -0.136, $p = 0.341$).

Figure 4. Plot illustrating the number of pollen morphotypes in Holocene pollen assemblages at latitudes from 0° to 78°N. This relationship is statistically significant (Kendall's Tau = -0.495, $p < 0.001$).

Figure 5. Plot illustrating the morphological diversity of Holocene pollen assemblages at latitudes from 0° to 78°N. Morphological diversity measured by mean pairwise Hamming distance. There is no statistically significant relationship between these two variables (Kendall's Tau = 0.092, $p = 0.508$).

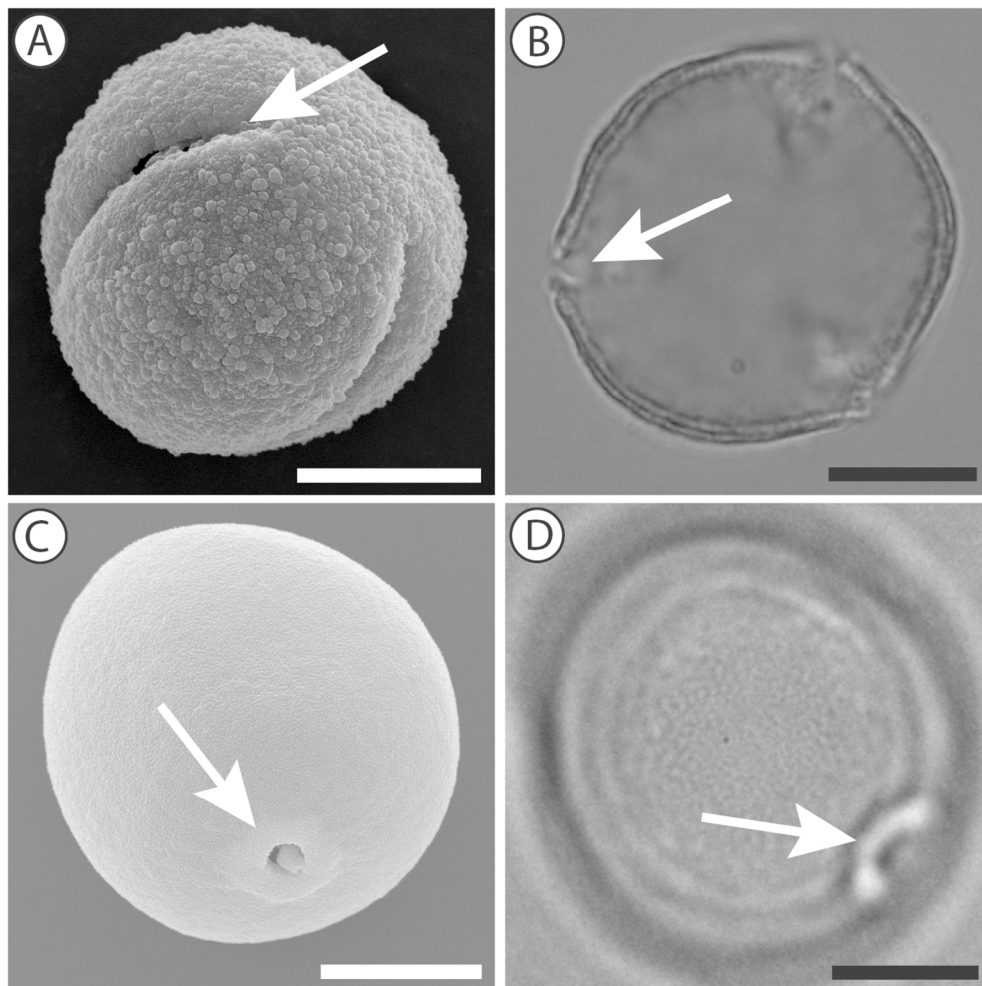
Figure 6. Dotchart illustrating how the morphological diversity of Holocene pollen assemblages grouped into biomes varies with latitude. Morphological diversity measured by mean pairwise Hamming distance. Only six datapoints are visible in the Tundra biome because Fish Lake and Hebron Lake have identical morphological diversity (0.458; see Table 1). The differences in morphological diversity across these five biomes are statistically significant (Kruskal-Wallis = 10.176_{3, 5, 6, 5, 7}, $p = 0.038$).

Figure 7. Barchart illustrating that the Tundra and Tropical biomes have the greatest proportion of endemic pollen morphotypes: 34% and 78%, respectively. See Table 2 for further information.

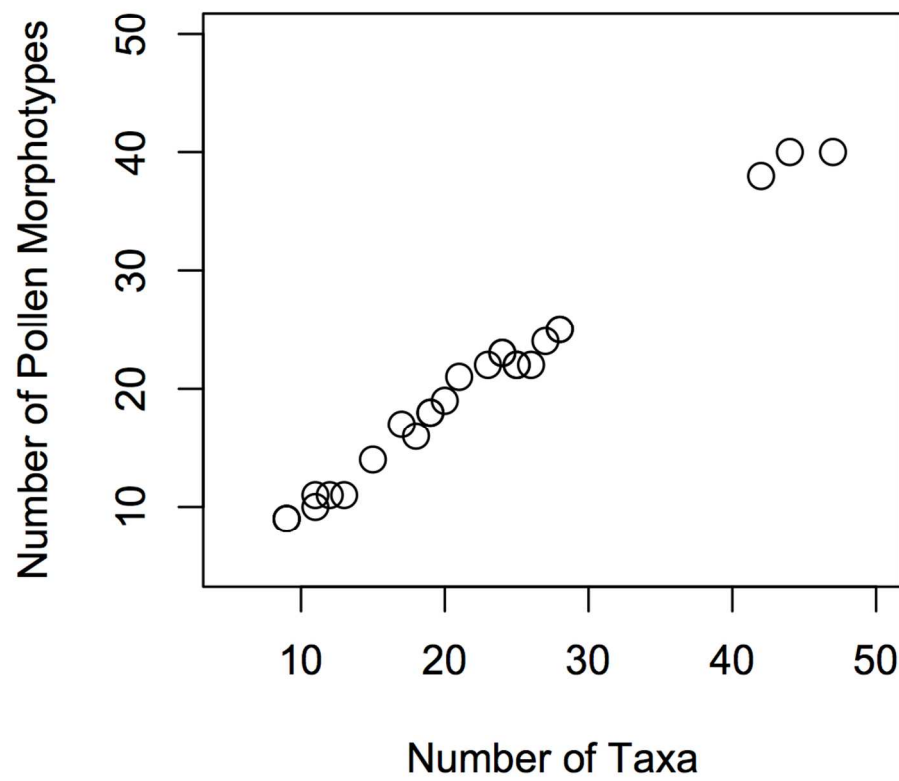
Table Captions

Table 1. Summary of the samples investigated in this study, together with the number of pollen morphotypes and measures of the morphological diversity of each sample pair. Biome classification Tundra (>56°N), Boreal (46–56°N), Temperate (36–46°N), Subtropical (23–36°N), and Tropical (three samples from 0°–5°N) follows Harrington (2004).

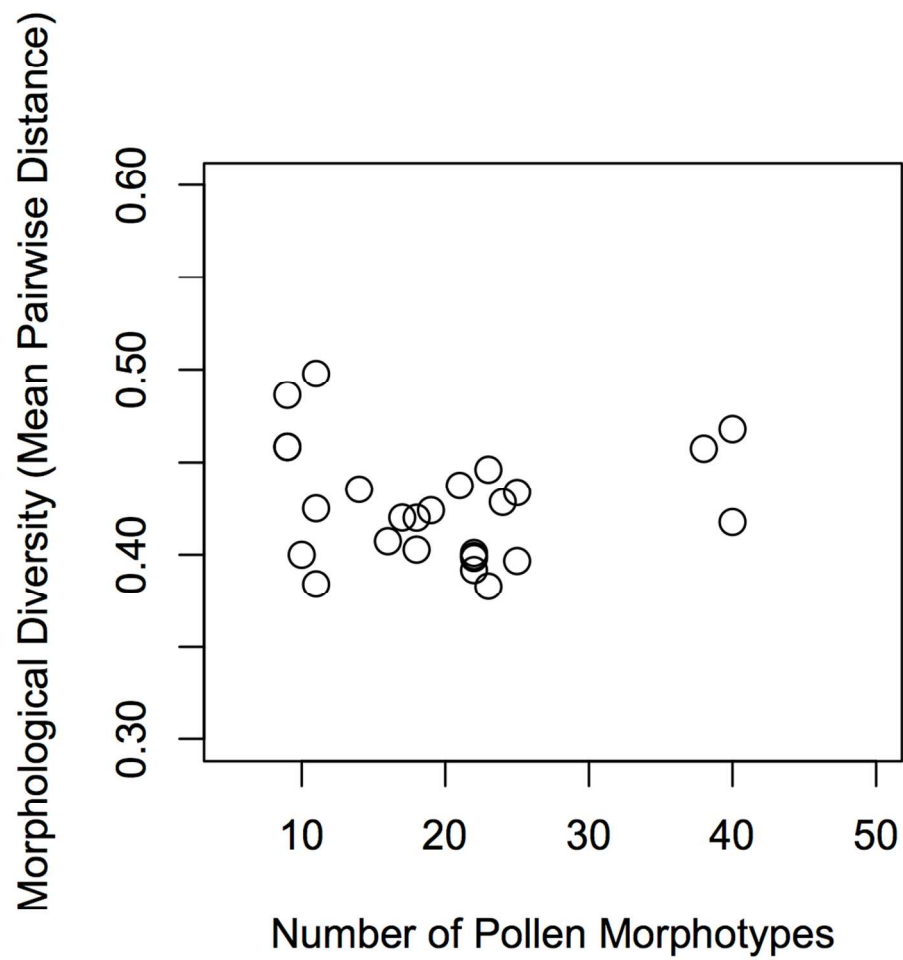
Table 2. The distribution of pollen morphotypes among the five biomes investigated here, and the morphological diversity of each biome as recorded by pollen grains.



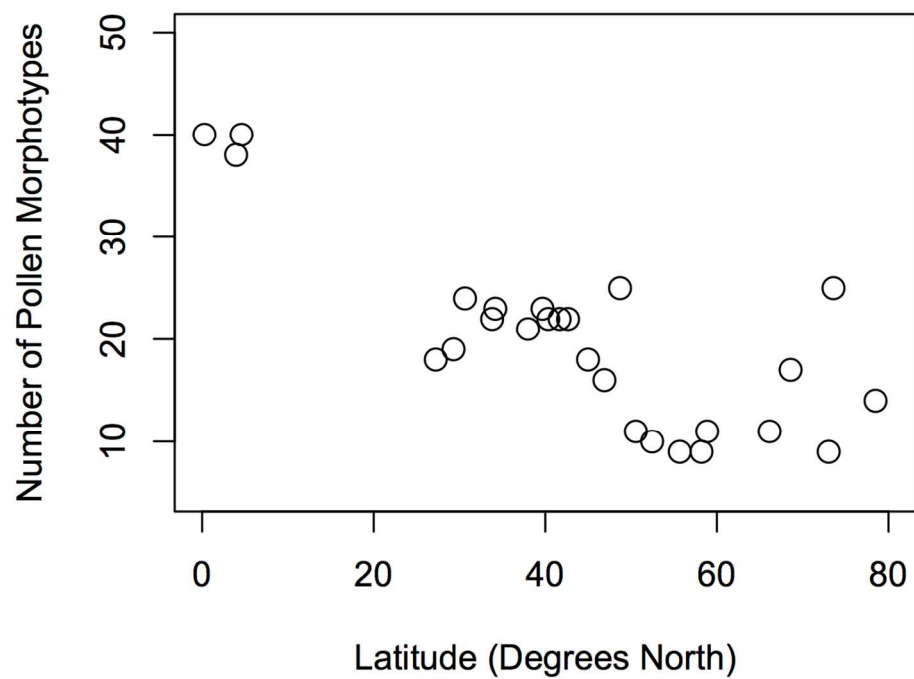
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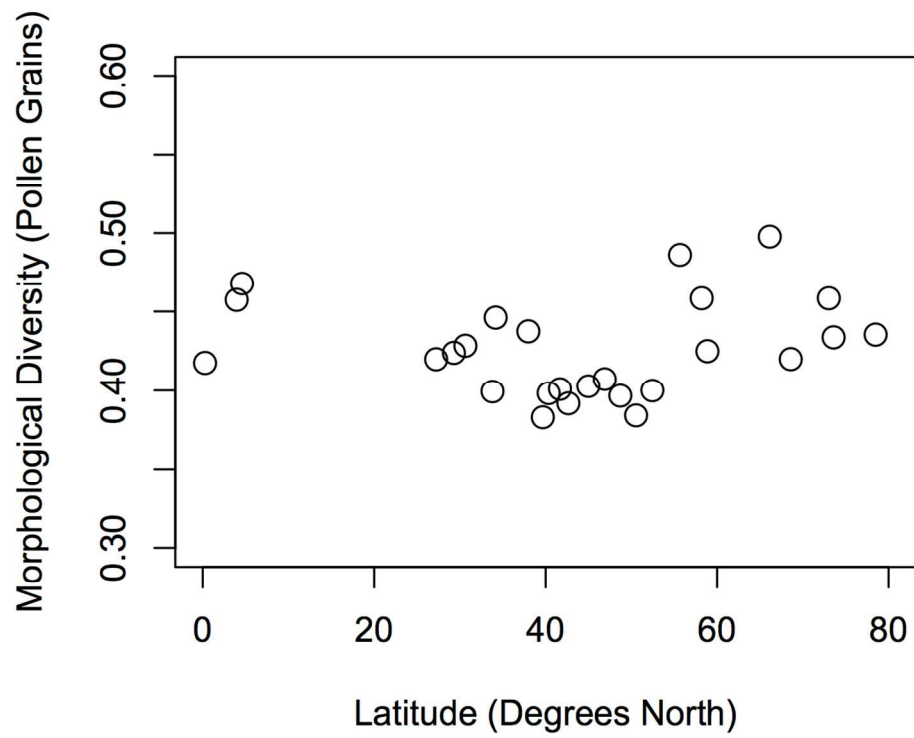
104x106mm (300 x 300 DPI)



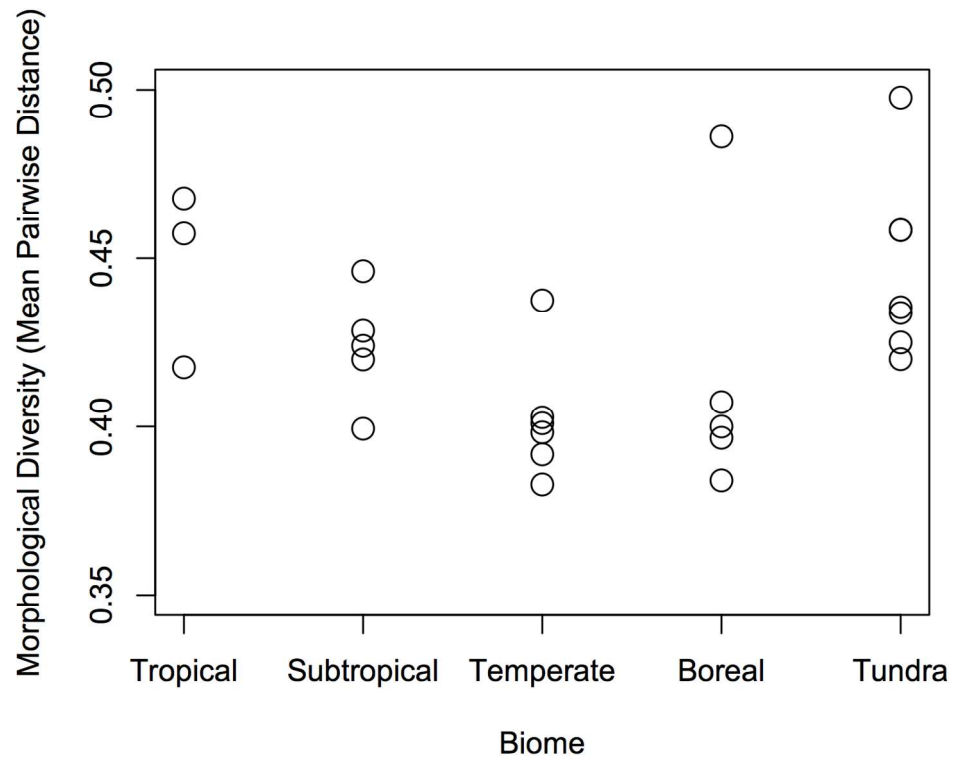
103x108mm (300 x 300 DPI)



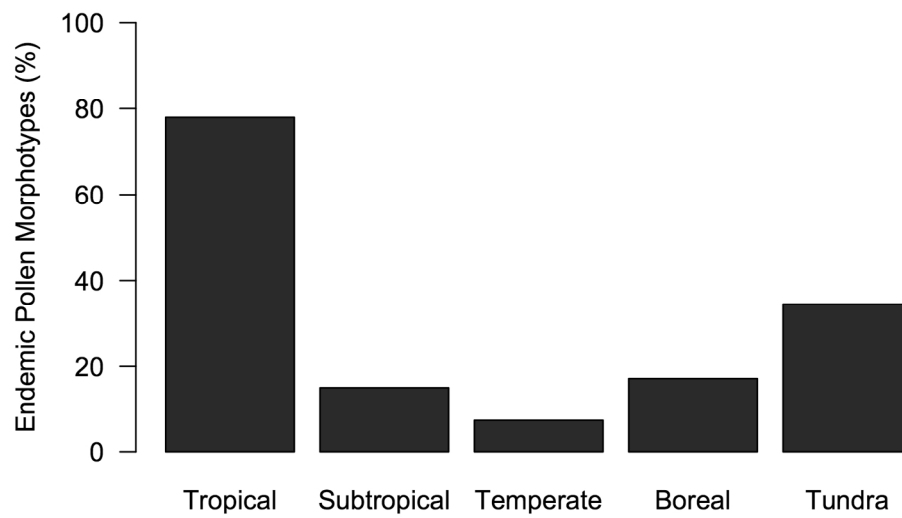
121x107mm (300 x 300 DPI)



121x108mm (300 x 300 DPI)



139x122mm (300 x 300 DPI)



160x115mm (300 x 300 DPI)

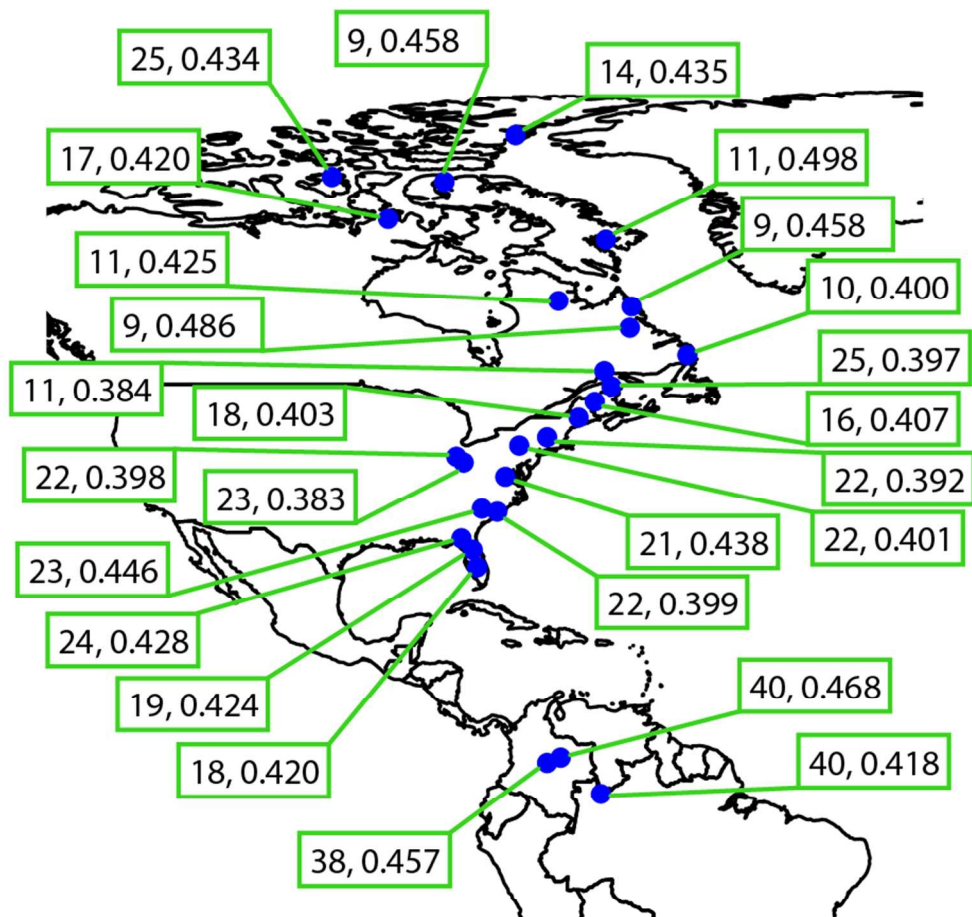
Site name	Latitude	Longitude	Samples (n)	Sample Ids (Neotoma)
Baird Inlet	78.49	-76.78	2	2182, 2183
Lake PWWL	73.59	-98.54	2	29076, 29077
Fish Lake	73.03	-85.22	2	17223, 17224
Lake SL06	68.59	-91.89	2	191395, 191396
Iglutalik Lake	66.14	-66.08	2	23518, 23528
Lac Faribault	58.87	-71.71	2	16874, 16879
Hebron Lake	58.2	-63.03	2	22124, 22125
Caribou Hill	55.67	-63.25	2	7721, 7724
Lake Hope Simpson	52.45	-56.43	2	31153, 31156
Lac Petel	50.55	-66.27	2	39991, 39992
Lac Triangle	48.71	-65.41	2	197013, 197015
Roulston Lake	46.89	-67.4	2	148756, 148757
Gould Pond	44.98	-69.32	2	19564, 19568
North Pond	42.65	-73.05	2	37452, 37453
Spring Lake	41.67	-76.35	2	49862, 49863
Silver Lake	40.35	-83.8	2	48564, 48566
Stages Pond	39.67	-82.94	2	50405, 50407
Hack Pond	37.98	-78	2	20933, 20934
White Pond	34.17	-80.78	2	63533, 63534
Clear Pond	33.8	-78.95	2	10025, 10031
Langdale Pond	30.64	-83.2	2	29386, 29388
Mud Lake	29.3	-81.87	2	36208, 36210
Buck Lake	27.23	-81.33	2	6734, 6735
Laguna Chenevo	4.59	-71.44	2	198500, 198504
Laguna Mozambique	3.96	-73.05	2	198475, 198479
Lagoa das Patas	0.27	-66.68	2	12933, 12934

Sample Age (Ka)	Biome	Pollen	Morphological Diversity
		Morphotypes (n)	(Mean Pairwise Hamming Distance)
2629, 3141	Tundra	14	0.435
2558, 3220	Tundra	25	0.434
2997, 3502	Tundra	9	0.458
2536, 2626	Tundra	17	0.420
2534, 3429	Tundra	11	0.498
2646, 3258	Tundra	11	0.425
2635, 3294	Tundra	9	0.458
2666, 3449	Boreal	9	0.486
2695, 3500	Boreal	10	0.400
2794, 3175	Boreal	11	0.384
2513, 3212	Boreal	25	0.397
2618, 3152	Boreal	16	0.407
2524, 3278	Temperate	18	0.403
2778, 3142	Temperate	22	0.392
2808, 3217	Temperate	22	0.401
2537, 3191	Temperate	22	0.398
2725, 3401	Temperate	23	0.383
2644, 3085	Temperate	21	0.438
2823, 3315	Subtropical	23	0.446
2655, 3477	Subtropical	22	0.399
2851, 3363	Subtropical	24	0.428
2546, 3476	Subtropical	19	0.424
2679, 3336	Subtropical	18	0.420
2520, 3321	Tropical	40	0.468
2513, 3456	Tropical	38	0.457
2762, 3314	Tropical	40	0.418

**Morphological Diversity
(Maximum Hamming
Distance Range)**

0.750
0.750
0.750
0.750
0.750
0.750
0.750
0.750
0.750
0.750
0.750
0.750
0.750
0.750
0.750
0.750
0.625
0.750
0.750
0.750
0.875
0.750
0.750
0.875
0.875
0.750

	Tropical	Subtropical	Temperate	Boreal	Tundra
Pollen Morphotypes (n)	68	40	41	35	29
Endemic Morphotypes (n)	53	6	3	6	10
Endemic Morphotypes (%)	77.94	15.00	7.32	17.14	34.48
Morphological Diversity (Mean Pairwise Hamming Distance)	0.448	0.427	0.417	0.404	0.434
Morphological Diversity (Maximum Hamming Distance Range)	0.875	0.875	0.750	0.750	0.750



80x80mm (300 x 300 DPI)